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Title: Chronic fertilization and irrigation gradually and increasingly restructure grassland communities

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Abstract

Scientists have known for over a century that resource addition can lead to species loss from plant communities. Recent studies have also shown that resource addition can substantially restructure communities by altering their functional and taxonomic composition – even when species richness remains unchanged. Understanding which aspects of community structure are impacted by different resources and over which timescales will provide insight for management decisions and may also elucidate which measures can act as early warning indicators for subsequent changes in the community. Here, we take advantage of a long-term factorial experiment to understand how grassland plant communities respond to a decade of nitrogen fertilization (14 g N m^{-2} $year^{-1}$) and irrigation (25 mm water $week^{-1}$ during the growing season). After 10 years, fertilization and irrigation decreased species richness by 27% and 11%, while functional trait diversity decreased by 55% and 35%. Abundance-weighted functional distance between treatments and controls increased by 55% and 24%, respectively. We expected that abundance-weighted measures would shift before presence-absence based measures, but found limited evidence for this. Instead, our results suggest that species gains, which can occur quickly because they require the addition of only one individual, may serve as early indicators for subsequent community restructuring. Overall, both chronic nitrogen fertilization and irrigation tended to have gradual and increasing impacts on community structure, but the magnitude of these effects varied greatly depending on the aspect of community structure investigated. Further study will be needed to determine the extent to which our results can be generalized to other resources or sites in order to develop management strategies to maintain both taxonomic and functional trait diversity in the face of chronic resource changes.

Key words: Community structure, diversity, functional traits, nutrient addition, temporal trends, water addition

Introduction

Ecosystems are continually confronted with many long-term and directional changes in the supply of the major resources required by plants, including various nutrients (Galloway et al. 2004, IPCC 2014), water (Huntington 2006, Zhang et al. 2007), and CO_2 (IPCC 2014). Increased resource supply can restructure terrestrial plant communities (Lawes et al. 1882, Suding et al. 2005, Harpole et al. 2016) by altering functional and taxonomic richness, abundance, dominance, and composition. This community restructuring often occurs at the expense of species that would otherwise be dominant under low resource conditions, where they are able to drive resources down to levels at which their competitors can no longer replace themselves (Tilman 1982, Dybzinski and Tilman 2007). When resources are added, these low resource levels will be exceeded and another resource will instead become limiting, leading to shifts in species dominance and composition over time (Dybzinski and Tilman 2007, Isbell et al. 2013b). This raises several so far unanswered questions: (1) will changes in resource supply quickly restructure communities and have consistent and persistent effects, or instead restructure communities gradually and increasingly over time (Hillebrand et al. 2008, Smith et al. 2009, Mouillot et al. 2013b)? and (2) do some resources, or combinations of resources, have a greater influence on community structure than others (DeMalach et al. 2017)?

Community restructuring by chronic resource addition could have several possible temporal trends. Building on the framework proposed by Smith and colleagues (2015), we outline several distinct hypotheses about these temporal trends and their implications for communities (Fig. 1).

First, if the structure of a community is largely determined by factors other than resource supply (e.g., herbivory, pathogens, temperature; Cleland et al. 2011), community responses to increases in resource supply could vary from one year to the next, appearing temporally stochastic (H1– stochastic effect). On the other hand, if community structure is largely determined by resource limitation, community responses to increases in resource supply could grow, either linearly or non-linearly, over time as favored species increase in abundance and those disadvantaged decline (H2 – gradual effect). This would lead to increasing differences between regions which either experience this pressure or not. Alternatively, a community could restructure rapidly once the resource addition exceeds a threshold (H3- abrupt change; Bestelmeyer et al. 2011, Isbell et al. 2013). After reaching this threshold, the community may either continue to change or persist in its altered state. Finally, chronic resource addition may have a transient effect, where the community structure changes for a brief time before returning to its initial conditions (H4 – transient effect). These transient effects dynamics may happen if species have time to acclimate to the increased resource supply so that even if new species can become dominant over short timescales, original composition will recover over longer time scales (Reich et al. 2018).

Different aspects of community structure may respond differently to a change in resource supply or follow different temporal trends (Smith et al. 2009, Mouillot et al. 2013b). For example, metrics weighted by species' abundances, including many trait-based metrics, may be more responsive than presence-absence metrics, such as species richness (Smith et al. 2009, Mouillot et al. 2013b). However, many studies have only separately investigated either the effects of chronic nutrient addition on the species richness of grassland plant communities (Willems et al. 1993, Stevens et al. 2004, Clark and Tilman 2008, Harpole et al. 2016), or the divergence or convergence of species (Inouye and Tilman 1988, 1995, Houseman et al. 2008,

93 Avolio et al. 2015) and functional (Weiher et al. 1998, Laliberte et al. 2013, Mason et al. 2013,
94 La Pierre and Smith 2015) composition. Using both taxonomic and functional trait metrics may
95 not only provide insight into the temporal trends of community structure response but also give a
96 more comprehensive picture of the extent of community restructuring.
97 Considering how both functional and taxonomic metrics respond through time can give
98 insight into exactly what is driving changes perhaps concurrent changes in other metrics. For
99 example, differences in species richness indicate changes in the number of species, but do not
100 provide information regarding whether the species gained or lost are similar to or different from
101 the original community. In contrast, changes in functional richness indicates that the species
102 gained or lost were functionally unique (i.e., had different traits than the original species) or were
103 replaced by functionally dissimilar or similar species (Cornwell et al. 2006, Villéger et al. 2008,
104 Boersma et al. 2016). Yet, such patterns in functional richness could be generated both by
105 concurrent changes in species richness or by species composition turnover (Fig. 2; e.g. Mayfield
106 et al. 2010). Likewise, turnover in functional or taxonomic composition as well as shifts in
107 relative abundances could occur without affecting functional or species richness indices (Fig. 2).
108 Therefore, by using both functional trait metrics and traditional taxonomic community metrics
109 we can more fully characterize how communities respond to different resource additions (Mason
110 et al. 2005, Boersma et al. 2016) and the temporal trends of these responses (Smith et al. 2009,
111 Mouillot et al. 2013b).
112 The objective of this study is to determine the extent to which temporal trends in community
113 restructuring depend on the type of resource added and the metric of community structure
114 investigated. Here, we examine temporal trends in the effects of chronic addition of water and
115 nitrogen– two commonly limiting plant resources – on grassland plant community structure,

including multiple aspects of taxonomic and functional composition. We use a 10-year, full factorial water and nitrogen addition experiment at Cedar Creek (East Bethel, MN, USA)(Yang et al. 2018). We consider changes in several aspects of community structure: species richness and evenness, functional trait means and variance (functional dispersion, functional richness, and functional distance), community-weighted means of traits, and species and functional group abundances.

Methods

Study system

This study was conducted at Cedar Creek Ecosystem Science Reserve, East Bethel, MN, USA. Soils at Cedar Creek are characterized as nutrient-poor entisols derived from a glacial outwash sand plain (Tilman 1987). Average wet N deposition rates are ~0.6 g N m^{-2} $year^{-1}$ (58% NH_4, 42% NO_3) (Clark and Tilman 2008). According to Köppen and Geiger classification (2006) the climate is characterized as cold continental with hot summer, but without dry season (Peel et al. 2007). The mean growing season (May – August) precipitation is approximately 420 mm, mean minimum growing season temperature is 12°C, and mean maximum growing season temperature is 25°C (1982-2016 period; http://www.cedarcreek.umn.edu/research/data). Plots are burned every year and fenced to prevent deer herbivory.

Experimental design

Thirty-six 9 x 9 m plots were planted with the same mixture of 32 grassland species in early spring of 1994 and again in 1995 (Tilman et al. 1997). Starting in 2007, plots were randomly assigned to one of six treatments, which included all combinations of two water treatments

(ambient and +25 mm/week during the growing season) and three nitrogen fertilization treatments (ambient, + 7 g N m^{-2} $year^{-1}$), or +14 g N m^{-2} $year^{-1}$). This water addition increases the total amount of water by ~80% during the average growing season, while the N fertilization rates are at levels relevant for understanding the impact of global wet deposition (Clark and Tilman 2008) and agricultural fertilization rates, respectively. Water was added to plots weekly from May to September via a sprinkler system, and nitrogen was added once in the beginning of each growing season as NH_4NO_3 (Farrior et al. 2013, Yang et al. 2018). Here, we show results from four of these treatments to simplify presentation (ambient, + water, + 14g N, and +water +14g N, n = 24), but similar results were obtained using both N addition treatments or grouping the N addition treatments together (Table S1). During 2007, 2008, 2010, 2015, and 2016, biomass from 4 strips, each 10 cm x 600 cm, was harvested, sorted to species, dried, and weighed. Non-planted species (weeds) were not removed from these plots, resulting in a total of 37 unplanted species observed across all plots and years. Overall, 96% of the biomass sampled across all plants and years was from the original 32 planted species.

Taxonomic metrics

We determined species richness (i.e. the number of species in a plot), inverse Simpson's evenness (Simpson 1949), and relative abundances of each species based on the harvested biomass from each plot. The biomass of the ten most abundant species over all plots and experiment years comprised ~82% of all biomass sampled. These ten species were: *Andropogon gerardii* (29.4%), *Sorghastrum nutans* (9.8%), *Schizachyrium scoparium* (8.5%), *Poa pratensis* (8.4%), *Lupinus perennis* (6.8%), *Dalea purpurea* (5.6%), *Coreopsis palmata* (3.9%), *Bouteloua gracilis* (3.1%), *Liatiris aspera* (3%), *Solidago rigida* (2.9%). For analyses of individual species'

biomass, the square-root of the biomass was used as the response variable in order to meet model assumptions of normality.

Functional traits

We characterized each species by four different functional traits which can be indicative of success when resource supplies increase (Craine et al. 2002, Sandel et al. 2010, La Pierre and Smith 2015). We included plant height (m) because it is associated with the ability to compete for light resources (Gaudet and Keddy 1988, Westoby 1998) and two leaf economics traits (specific leaf area (SLA), $mm^2\ mg^{-1}$ and leaf tissue nitrogen per dry mass (leaf N), $mg\ g^{-1}$) because they are associated with the trade-off between acquisitive, fast-growing, but short-lived leaves and conservative, slow-growing, but long-lived leaves (Wright et al. 2004, Reich 2014). We also included photosynthetic pathway (C3/C4) because it is related to seasonality and resource use efficiency. Trait data were obtained from Cedar Creek datasets (http://www.cedarcreek.umn.edu/research/data) and the global plant trait database – TRY (Kattge et al. 2011; www.try-db.org, see Table S2 for a summary of data used and associated references). We averaged each trait over all records for each species when more than one observation existed in the databases. Over half of the species had more than 10 observations, and dominant species had from 50 – 650 observations. Species missing information for more than two traits were excluded from trait-based analyses, though we were able to characterize between 87 – 100% of species and 89 - 100% of biomass present in each treatment and year with available data (Table S3). While species may shift their trait values in response to changing environmental conditions (Lepš et al. 2011), species reordering, gains and losses are expected to dominate community responses over the longer timescales of our experiment (Smith et al. 2009).

185 Thus, characterizing species by average values captures changes in the *types* of species but not
186 intraspecific trait responses.
187
188 *Functional trait metrics*
189 We calculated three different functional trait metrics; each testing a specific aspect of functional
190 composition response to increases in resource supply. First, functional richness measures the
191 amount of trait space occupied by a community based on the presence or absence of traits,
192 regardless of their relative abundance in the community (Mason et al. 2005, Cornwell et al.
193 2006). Significant decreases in functional richness indicate convergence toward a similar trait
194 composition (Laliberte et al. 2013, Mason et al. 2013, Boersma et al. 2016). Functional richness
195 is calculated as the convex hull of the multivariate trait space, the multidimensional space where
196 each axis corresponds to a trait. Second, functional dispersion quantifies the spread of traits in
197 the community based on both presence and relative abundances (Laliberte and Legendre 2010).
198 Significant changes in functional dispersion, without parallel changes in functional richness, can
199 indicate shifts in trait dominance and evenness (Boersma et al. 2016). Functional dispersion is
200 calculated as the abundance-weighted average of the distance that each species (trait
201 combination) is away from an abundance-weighted centroid of the community (i.e., within a
202 plot) (Laliberte and Legendre 2010). Third, functional distance indicates whether treated plots
203 are located in different areas of trait space compared to ambient plots (Boersma et al. 2016).
204 Functional distance is calculated as the distance between the centroids of each pair of plots to
205 determine whether distances between pairs of plots within the same treatments are less than those
206 between treatments (*see* Boersma et al. 2016). In our analyses, increases in functional distance
207 through time indicate shifts in species abundance and species turnover, such that treatment plots

are moving further away from ambient plots in trait space. For each trait, a community-weighted mean and a non-weighted mean was calculated for each plot at each year to investigate which *types* of species (e.g., do we tend to move towards species with high tissue nutrient concentration?) were responding based on abundance and presence/absence. Lastly, we also grouped species into four functional groups based on broadly similar physiology and morphology - C4 grasses, C3 grasses, legumes, and all other non-legume forbs- to classify how these groups respond to our treatments. These functional groups have been previously shown to be responsive to long-term nutrient addition (Tilman et al. 1997, Reich et al. 2004).

We calculated functional richness and dispersion for each plot within each year using the FD package in R (Laliberte and Legendre 2010, Laliberté et al. 2015). We did the analyses with both *z*-transformed and untransformed trait values. There were no qualitative differences between the two methods, so we present data using untransformed trait values. We set $m = 4$ to compute functional richness since we characterized each species by 4 different traits. We calculated functional distance based on abundance-weighted and non-abundance-weighted distances between plots to assess the extent to which results depended on shifts in relative abundance, rather than changes in the presence or absence of species (Boersma et al. 2016); see *Statistical analyses* for a discussion on how this was modeled.

Statistical analyses

To determine how functional and taxonomic metrics responded to treatments, our estimated models considered (1) the three-way interaction of each treatment and experiment duration, (2) all pair-wise interactions, (3) the main effect of each treatment and study duration. The models also accounted for effects of average annual biomass production and the standardized

231 precipitation-evapotranspiration index (SPEI, Fig. S1). We build off of previous frameworks for
232 testing temporal trends (Smith et al. 2009, 2015), but determine temporal trends from statistical
233 models which represent our hypothesized relationships and AIC model selection. Reflecting our
234 hypotheses about temporal trends, we consider three candidate functional forms for the
235 interaction between nutrient treatment, irrigation treatment, and experimental duration: linear
236 (gradual response; H2), log-linear (gradual response; H2), and quadratic (transient response; H4),
237 along with year as a factor (stochastic response; H1). If there were only main effects for the
238 treatments, we considered this a threshold response (H3). We included the average biomass
239 production each year and the standardized precipitation-evapotranspiration index (SPEI;
240 Vicente-Serrano et al. 2010) for the 5-month growing season (April – August) to control for their
241 effects and get more precise estimates of the treatments effects on measures of community
242 structure. Model selection was based on the lowest AIC for the results shown, with Δ AIC > 2
243 (Table S1). If the 3-way interaction between the two treatments and year was not significant, it
244 was removed for parsimony (Crawley 2013). We removed SPEI and biomass only if this
245 improved AIC values by Δ AIC > 2, which occurred only for SLA. Reflecting our hypotheses
246 about temporal trends, if the quadratic form fit best, but had no treatment by year^2 interactions
247 (e.g. no transient effect), the next best model was used.
248 To account for plot-by-plot variability, we considered models that included random
249 slopes for each treatment and random intercepts for each plot. After model selection, we used
250 random intercept only models, which had the lowest AIC values (Δ AIC > 5). To account for the
251 repeated measures through time, we used compound symmetry covariance structures (Pinheiro
252 and Bates 2000). All models selected had the compound symmetry structure. We were unable to
253 consider other temporal covariance structures, such as a first-order autoregressive structure,

because data were not collected every year. All analyses were completed in R v 3.3.3 (R Core Team 2017) using the lme function in the nlme package (Pinheiro et al. 2017).

We modeled both abundance-weighted and non-abundance-weighted functional distance as outlined in Boersma et al (2016) using the MCMCglmm package in R (Hadfield 2010). We compared ambient plots to all treatment plots to determine whether increased resource supply causes communities to move to a different area of trait space. We constructed a trait matrix that included all species present for all years and an abundance matrix for all years to calculate centroids and distances between plots in multidimensional trait space (see Boersma et al 2016). We then selected for only within year distances. Comparisons were made between ambient plots and all treatment plots to determine how treatments impacted trait shifts. To account for the multiple comparisons between plots within each year, we modeled random effects as a multi-membership model where variance is equally distributed across all pairs of plots within each year. We also included average biomass for each year and the 5-month SPEI in our models to more accurately predict the impacts of the specific treatments on functional distance. The best model for the abundance-weighted distances included SPEI and biomass (Fig. S1). The best model for the natural logarithm of non-abundance-weighted distances included year as a factor (Fig. S2).

Results

Overall, we found that fertilization and irrigation caused most measures of community structure to gradually deviate from ambient plots, and these effects increased through time (Table 1, H2). Over the duration of the experiment, fertilization and irrigation impacted a similar number of community metrics. Under fertilization treatments 11 measures of community structure

277 responded with continuous gradual changes over time, four displayed stochastic (but directional)
278 changes, four changed abruptly, and one showed transient change. Under irrigation treatments,
279 12 measures of community structure exhibited continuous changes, five changed abruptly, three
280 showed transient change, and one responded stochastically (Table 1). The trends in the
281 community structure measures were often mirrored by species-specific and individual functional
282 trait responses, although not always.
283
284 *Taxonomic restructuring*
285 Fertilization rapidly increased species richness in the first year, but had a continuous negative
286 impact on species richness and Simpson's diversity over the duration of this experiment (Fig.
287 3A-B, Fig. S1; H2). Overall, fertilization decreased species richness by 27% and Simpson's
288 diversity by 45%. The effect of irrigation on species richness also increased over the duration of
289 the experiment, amounting to an 11% decrease (Fig. 3B, Fig. S1; H2). In contrast, irrigation did
290 not have a significant effect on Simpson's diversity (Fig. 3A, Fig. S1). Fertilization marginally
291 decreased evenness by 15% within the first year, and this effect persisted at approximately the
292 same magnitude during subsequent years (Fig. 3C, Fig. S1; H3).
293
294 *Functional restructuring*
295 Fertilization caused a stochastic decrease in functional richness over the duration of the
296 experiment; there was an overall decline in functional richness resulting in a 55% decrease
297 compared to ambient plots, but the magnitude of the effect was variable from year to year (Fig.
298 3D, Fig. S1; H1). Fertilization also caused functional composition to become increasingly
299 different from ambient plots over time when considering abundance weighted distances (Fig. 3F,

Fig. S1; H2) and caused a stochastic divergence when considering non-abundance-weighted distances (Fig. S2; H1). Thus, fertilization caused both a contraction of trait space and shifted the region of trait space occupied by each community (Fig. 2D). Irrigation also caused plots to diverge from ambient plots through time, but only when considering abundance-weighted distances (Fig. 3F, Fig. S1). Functional dispersion did not respond to any of the treatments and remained relatively consistent through time (Fig. 3E, Fig. S1).

Community-level functional responses

Functional group composition was influenced by both nitrogen addition and irrigation (Fig.4 and 5, Table S4). Fertilization had a rapid and persistent effect on the proportion of the community represented by legumes (negative) and C3 grasses (positive; H3), and had gradual continuous effects on the proportion of non-legume forbs (negative) and C4 grasses (positive; Fig. 4A-D; H1). The decrease in non-legume forbs was mirrored by a continuous decrease in the proportion of the community weighted mean proportion of C3 species and height (Fig. 4G-H, Table S6). Irrigation had positive, rapid and persistent impacts on the proportion of C4 grasses in the community (H3), decreased the proportion non-legume forbs and C3 grasses through time (H1), and increased the proportion of legumes through time (Fig. 4A-D, H1). Plots that were both fertilized and irrigated decreased in non-legume forbs less than expected from the additive effects of each treatment separately (Fig 4C). Changes in functional groups were mirrored by rapid decreases in community weighted means of leaf N and proportion of C3 species (Fig. 4F & H, Table S6). Most of the functional groups and community-weighted traits had rapid responses to at least one of the treatments in the first year of the experiment (Fig. 4, Table 1).

Species-specific responses

Irrigation caused changes in the biomass of eight of the ten most dominant species whereas nitrogen caused changes in biomass of seven of these ten species (Fig.5, Fig. S3). The most common response was a linear change through time (six of ten, H2). Species-specific responses reflected the trait and functional group responses. For example, fertilization had an increasingly positive effect on *Andropogon gerardii* biomass, a C4 species with low tissue N and moderately high SLA. In contrast, fertilization had an increasingly negative effect on *Lupinus perennis* biomass, a C3 legume with high tissue nitrogen (Fig. 5; see Fig. S3 for more details).

Discussion

Here, we show that temporal trends in the plant community response to chronic resource addition depend on both the resource and the specific aspect of community structure under consideration. In this experiment, we find that nitrogen fertilization and irrigation gradually and increasingly impacted many aspects of community structure. Few metrics had stochastic or transient responses, while some had abrupt responses. Increasing species loss over time with nutrient addition is consistent with other previous studies both at our study site (Clark and Tilman 2008, Isbell et al. 2013a) and globally (Stevens et al. 2004, Maskell et al. 2010, Harpole et al. 2016). We further show that several aspects of community structure had gradual and increasing responses to fertilization over time. Globally, the short-term effects of water addition on species richness is known to vary considerably across study sites, but has a positive effect on average on species richness (DeMalach et al. 2017). Our results suggest that the long-term effects of increased water availability on community structure may be discernable from short-term studies because gradual, continuous responses were common. While many metrics had this

346 gradual and continuous response to chronic resource addition, not all had the same temporal
347 trends.

348 Using multiple metrics of plant community composition allowed for a more comprehensive
349 understanding of community restructuring and allowed us to tease apart changes in certain
350 aggregate metrics. We found that both species richness and functional richness were declining in
351 fertilized treatments, providing evidence that fertilization causes not only species loss, but also
352 loss of functionally unique species. This effect is consistent with results from other sites (Suding
353 et al. 2005) and provides evidence that the species lost as a result of resource addition were those
354 with distinctive trait combinations. The loss of distinctive trait combinations can reduce
355 ecosystem stability and affect functioning, potentially reducing the range of conditions in which
356 the community can maintain high levels of productivity (Isbell et al. 2011, Mouillot et al. 2013a,
357 Violle et al. 2017). Alternatively, their disappearance could increase ecosystem stability if highly
358 stable species persist (Polley et al. 2007). Further, fertilized and irrigated plots occupy a different
359 region of trait space compared to ambient plots. Specifically, we found that both fertilization and
360 irrigation increased the abundance of species with higher SLA and decreased the abundance of
361 C3 species, whereas irrigation shifted communities towards species with lower leaf nitrogen,
362 which were consistent with some other studies (Sandel et al. 2010, La Pierre and Smith 2015, but
363 see Isbell et al. 2013b). This contraction of trait space may indirectly impact certain ecosystem
364 functions like productivity through time (Isbell et al. 2013a), if, for example, it reduces
365 complementarity between species (Loreau and Hector 2001, Fargione et al. 2007). It could also
366 potentially increase productivity by selecting for more productive species in the new
367 environmental context (Roscher et al. 2012, Cadotte 2017). More studies are needed to
368 understand the consequences of these trait shifts on ecosystem functioning.

We expected that abundance-weighted or functional trait metrics would shift before presence-absence based measures (Hillebrand et al. 2008, Mouillot et al. 2013b), but found limited evidence for this. Instead, our results also suggest that species gains, which can occur quickly because they require the addition of only one individual, may serve as early indicators for subsequent species losses, which often take more time because they require the loss of the last individual. While we found that many abundance-weighted metrics, including Simpson's diversity, evenness, and community-weighted means, can have rapid responses to chronic resource addition these metrics did not necessarily deviate much from ambient temporal trends through time, indicating limits to their sensitivity. Conversely, we saw a rapid increase in both species richness and functional richness within the first year that indicates functionally unique species were added to the community. Rather than turnover, these species were lost over the duration of experiment because many of the dominant species and functional groups tended to increase over time. Further, many of the functional groups responded rapidly to irrigation, and community weighted means of traits responded rapidly to both fertilization and irrigation. This suggests that the early-indicator metrics may differ from resource to resource. Nevertheless, it does not seem that abundance-weighted or functional trait metrics captured changes in community composition sooner than taxonomic measures.

Nitrogen and water are expected to restructure the community in different ways because of how these treatments were applied and how these resources interact within the system. In this experiment, are more comparable to agricultural levels of nitrogen fertilization than rates of atmospheric N deposition. Irrigation treatment levels increased water by 80% compared to average ambient precipitation levels over the past 30 years. Further, nitrogen was applied once at the beginning of the growing season whereas irrigation occurred weekly throughout the growing

season, so differences in resource addition frequency may cause differences in how plants compete for these resources. Irrigation likely reduced water stress throughout the season whereas nitrogen addition may have had a disproportionate impact on species establishment early in the growing season. Furthermore, nitrogen can accumulate in the system over multiple years (Isbell et al. 2013b) whereas although irrigation can alleviate water stress throughout the period of application, it is not retained by the sandy soils at our site, limiting the cumulative effect of chronic application. The resulting difference in effective resource availability over time, may help to explain why the effects of nitrogen were greater in magnitude at our site. Cedar Creek is strongly nitrogen limited, and adding nitrogen consistently increases aboveground plant biomass, reduces species richness, and shifts dominance (Tilman 1982, Clark and Tilman 2008, Isbell et al. 2013a). Nitrogen is therefore expected to have a greater effect on community structure than water availability, which is not a limitation at our site, except perhaps during droughts, rainfall being higher compared to many other grassland sites (Cleland et al. 2013). It follows that more xeric grasslands may have greater responses to water addition (Cleland et al. 2013, Wilcox et al. 2017). These experimental treatments could impact sites with different climates differently than what we found here, but we expect that gradual, continuous responses should dominate response to chronic pressures.

Environmental changes cause shifts in the functional structure of a community as the result of species replacement and within-species variation lead (Lepš et al. 2011). In this paper, we focused on the trait variability between species, i.e. using one average trait values for each species for all plots samples, variation between species is thought to be greater than variation within a single species (*but see* Albert et al. 2010, Moran et al. 2016). Further, we were interested in long term trends which are primarily related to species replacement (i.e. changes in

415 species composition or abundance). However, the use of average trait values can mask within
416 species variation, i.e., the variation between individuals exposed to different environmental
417 conditions (Smith et al. 2009). Therefore, using average trait values may conceal some changes
418 in community structure that could otherwise be detected by measuring traits for every species in
419 every treatment during every year (Jung et al. 2010, Violle et al. 2012). However, these
420 intraspecific differences are expected to be more important in the case of short term assessment
421 (Smith et al. 2009, Auger and Shipley 2013) when the taxonomic structure of the community is
422 more similar to previous states. There is still clearly a need to sort out how important
423 intraspecific trait variation is in determining community structure and over what time scales it is
424 relevant.

425 Overall, we found that chronic resource additions resulted in continuous, gradual changes in
426 communities, consistent with H2, and that nitrogen and irrigation impacted a similar number of
427 metrics. For metrics that responded to both fertilization and irrigation, fertilization had much a
428 larger effect size. While gradual and increasing changes were the most common, we found
429 evidence for each of our hypothesized trends under both treatments regimes. Because of this
430 array of responses, further research is needed to determine the extent to which our results can be
431 generalized to other resources or sites. Understanding these temporal trends at different sites and
432 for different resources will help inform our expectations for when and how much chronic
433 resource addition will modify communities. We will also be able to show what metrics are early
434 indicators of future change. Thus, discerning exactly when and where we expect these temporal
435 trends to occur will help us develop management strategies to maintain both taxonomic and
436 functional trait diversity in the face of these chronic resource changes.
437

Author Contributions:

KK – Conceived the project and performed the data analysis and led the writing

LD – Contributed to conceptualization of temporal trends and hypotheses, conceptual figures, analyses, and writing

DT – Designed experiment, contributed to writing

IA - Contributed to plant trait data and writing

GB - Contributed to plant trait data and writing

JC – Contributed to plant trait data and writing

JK – Contributed to plant trait data and writing

FI – Contributed to analyses and writing

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691 **Tables and Figures**

692 *Table 1*: Most metrics of community composition had continuous gradual responses to chronic
693 resource addition. Here, we show which hypothesis (Fig. 1) each metrics followed for nitrogen
694 fertilization (F, +14 g N m^{-2} $year^{-1}$), irrigation (I, +25 mm H_2O $week^{-1}$ May-September), or the
695 interaction of the two (F:I). Functional traits shifts were quantified both by community weighted
696 means and non-weighted (NW) means. Metrics were considered to have rapid responses, or
697 responses in the first year which distinguished them from ambient plots, if the standard error for
698 the treatment at year 1 did not overlap with ambient standard errors. Rapid responses were not
699 characterized for species-specific responses. Detailed results and estimated effects can be found
700 in Figs. 3, 4, & S1.

Metric	H1 – Stochastic	H2 – Gradual	H3 – Abrupt	H4 – Transient	Rapid Response
Community Metrics					
Species Richness		F, I			F
Simpson's Diversity		F			
Evenness			F		
Functional Richness	F				F
Functional Dispersion					
Functional Distance (AW)		F, I			
Functional Distance (NW)	F				
Functional Traits					
SLA					F, I
Leaf N			I		I
Height		F, F:I			F, I
Proportion C3		F	I		
SLA (NW)			F, I		F, I
Leaf N (NW)				I	
Height (NW)				I	
Proportion C3 (NW)		F, I, F:I			F
Functional Groups					
C4 Grasses		F	I		
C3 Grasses		I	F		I
Legumes		I	F		I
Non-legume Forbs		F, I, F:I			F, I
Dominant Species					
Andropogon gerardii	F, I				

Bouteloua gracilis				F, I	
Coreopsis palmata		I			
Dalea purpurea		I			
Liatris aspera		F, I			
Lupinus perennius		F			
Poa parentis			I		
Sorghastrum nutans		I			
Solidago rigida		F, I, F:I			
Schizachryum scoparium	F				
Total Responses:	F:4, I:1	F:11, I:12	F:4, I:5	F: 1, I:3	F: 7, I:7

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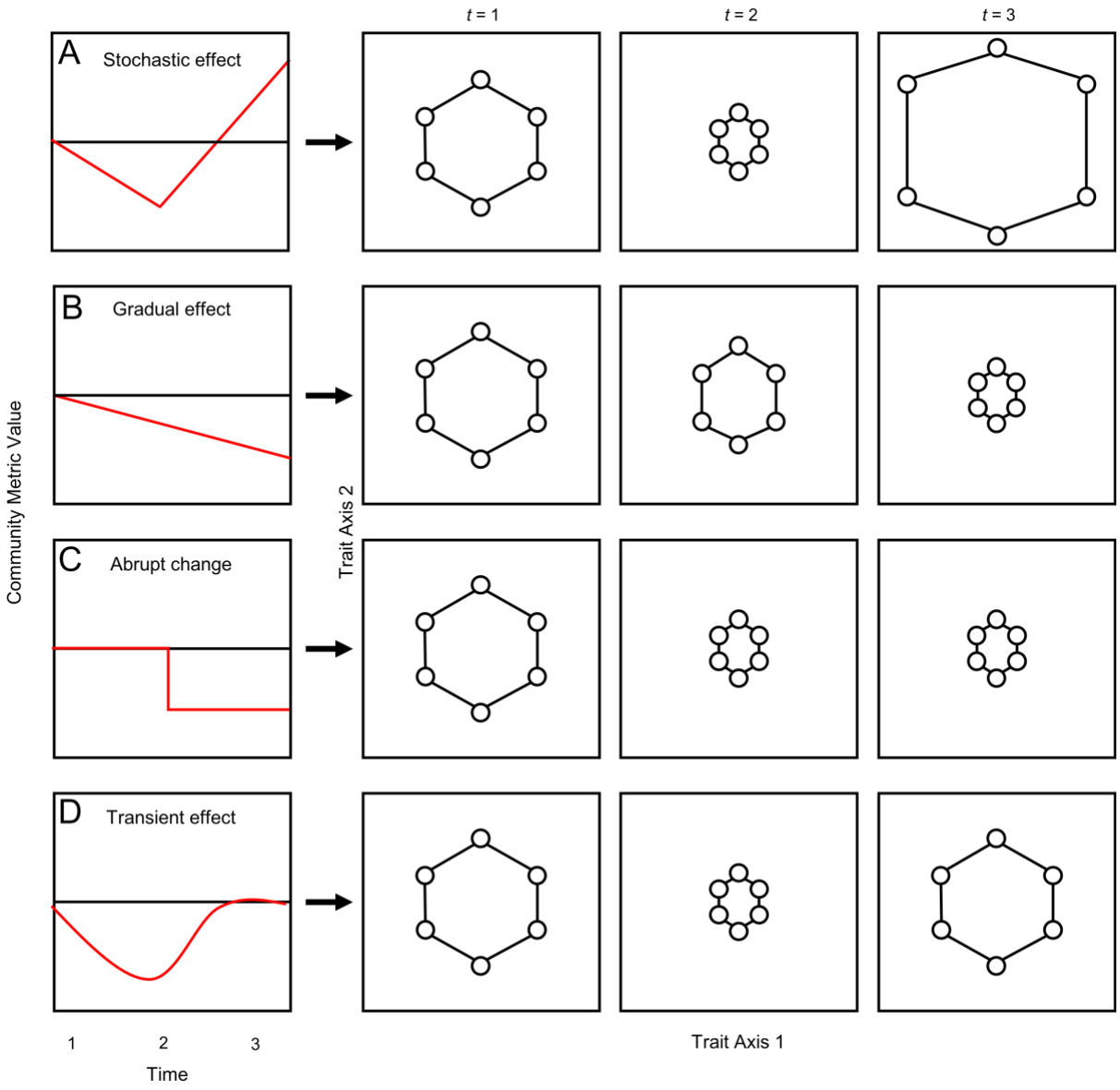


Figure 1: Graphical representation of how chronic resource addition can alter measures of community composition through time. In the simplest case where the ambient plots (black line) stay static through time, the solid red line is the hypothetical response to a chronic resource addition. Communities can either (H1) have random shifts ('stochastic effect'), (H2) increasingly deviate ('gradual change'), (H3) have a sudden, but persistent shift ('abrupt change'), or (H4) an initial effect that diminishes through time ('transient effect'). Functional richness responses are illustrated here, but we studied temporal trends in several metrics of community structure.

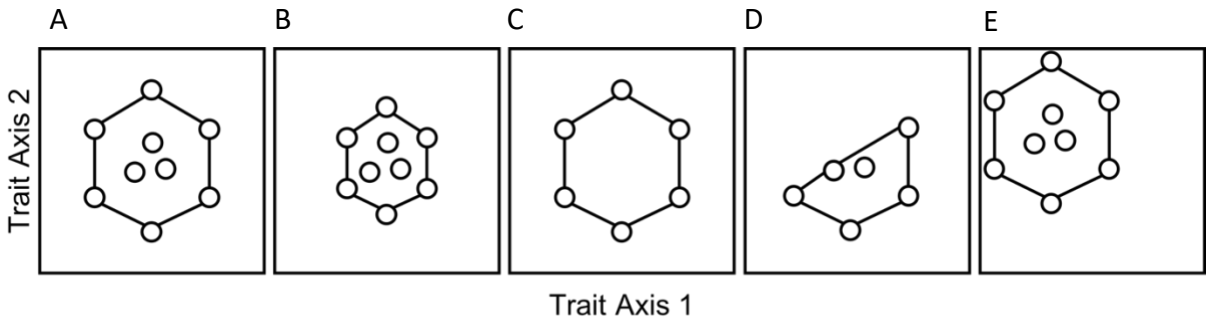


Figure 2: Multiple trait-based and taxonomic measures provide complementary information when characterizing community restructuring. We show several hypothetical responses of community (A), which is comprised of 9 species, to resource addition. Each circle is a species, plotted according to its trait values. Functional richness, the volume of the convex hull, is shown by the area inside of the connected species. For example, resource addition may have no effect on species richness, but decrease functional richness (B); or have no effect on functional richness, but decrease species richness (C); or decrease both species richness and functional richness (D); or decrease neither species richness nor functional richness, but shift the community to a different region of trait space, which can be captured by functional distance (E).

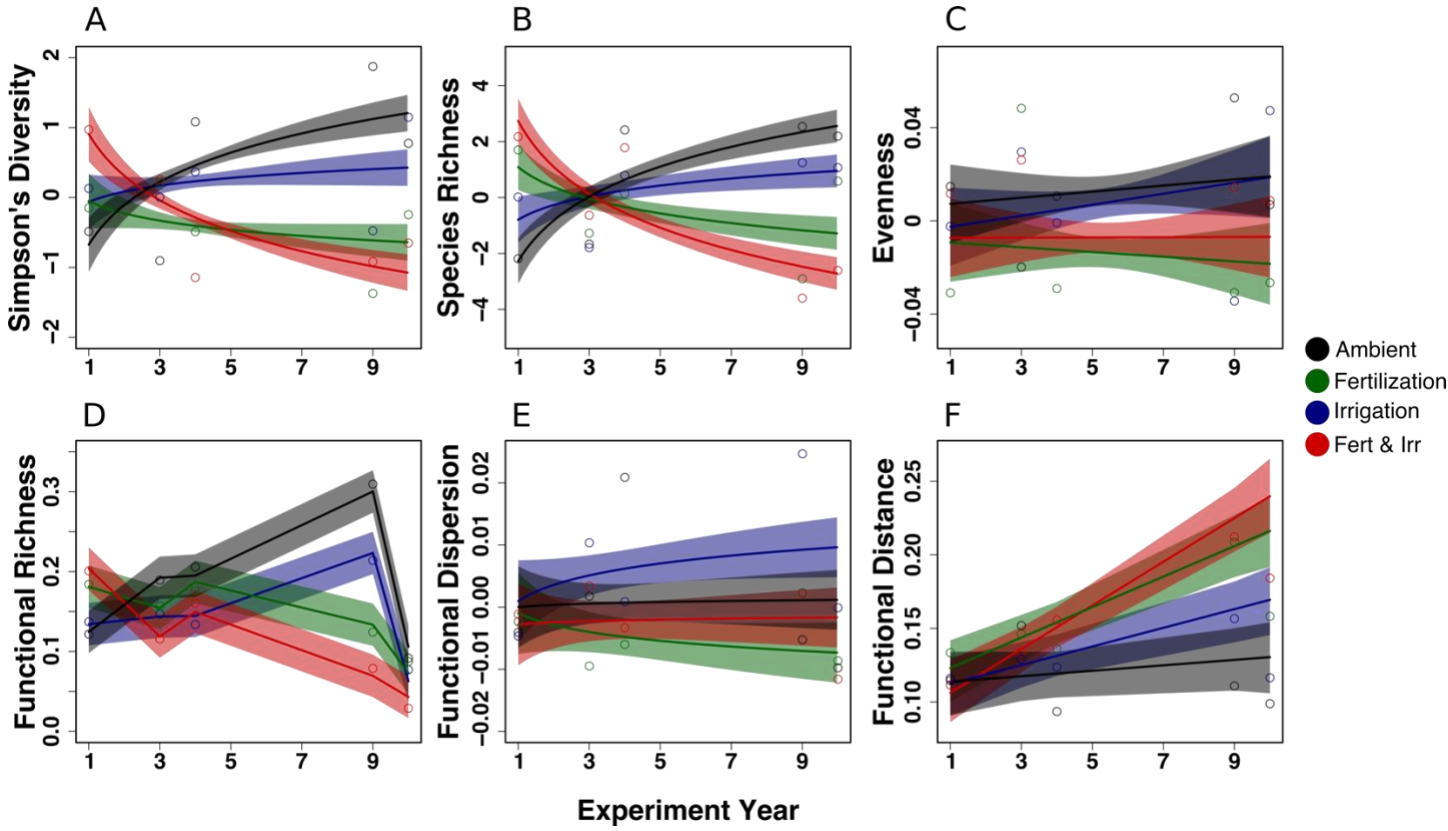


Figure 3: Fertilization (+14 g N/m^2/year) and irrigation (+25 mm H_2O/week from May-September) tended to cause gradual and continuous effects on plant community structure compared to ambient plots. Fertilization had increasingly negative effects on both Simpson's Diversity (A) and species richness (B), but had a significant abrupt effect on evenness (C). Irrigation only had an increasingly negative effect on species richness (B). Fertilization caused a stochastic decrease in functional richness (D). Irrigation and fertilization caused treated communities to become increasingly dissimilar from ambient communities (F) and did not impact functional dispersion (E). Y-axis values are residuals from partial regressions after accounting for SPEI and biomass, error bands show ± 1 standard error, points represent observed average values.

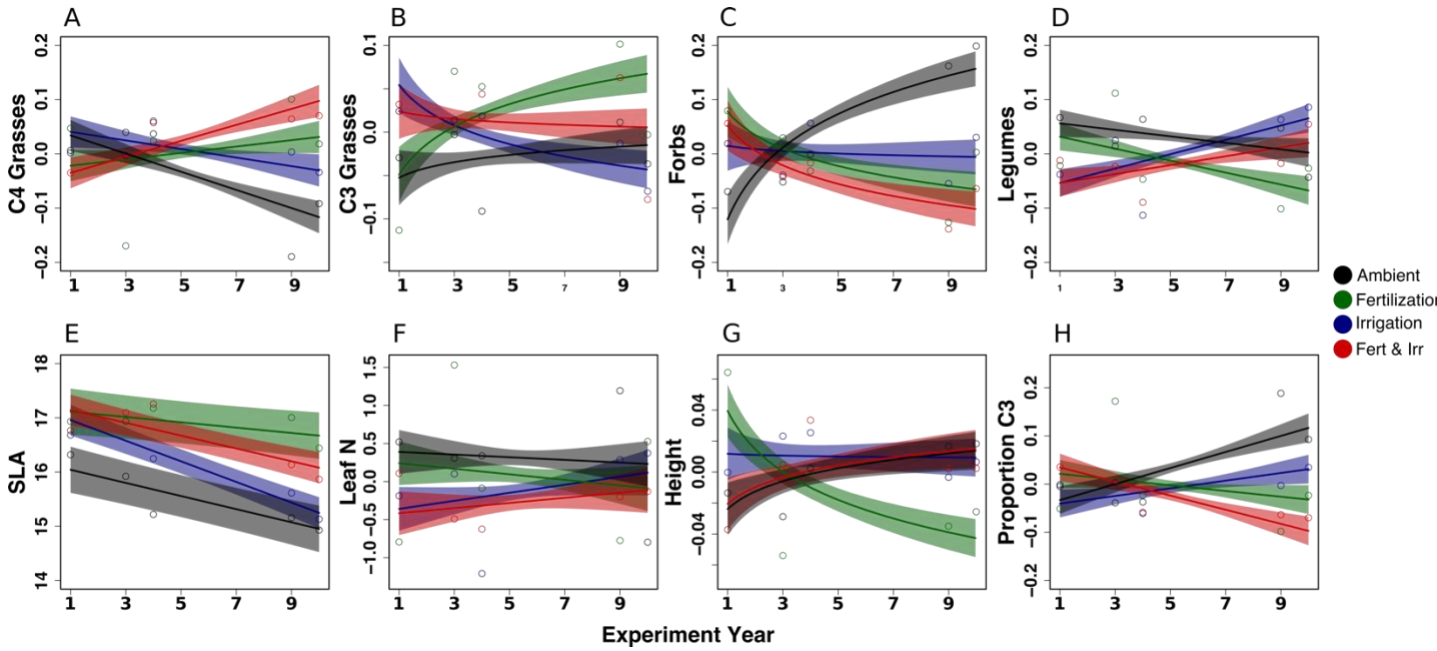


Figure 4: Both functional group composition (A-D) and functional traits (E-H) were influenced by fertilization (+14 g N/m^2/year) and irrigation (+25 mm H_2O/week from May-September). Fertilization and irrigation both had rapid impacts on functional groups(A-D), which then tended to diverge from ambient plot temporal trends. Fertilization tended to have gradual continuous effects on traits (E-H) and irrigation tended to have immediate and smaller persistent impacts. Y-axis values are residuals from partial regressions after accounting for SPEI and biomass, except for SLA, where these variables were not included in the model (Tables S4 & S5). Error bands show ± 1 standard error, and points are observed average values.

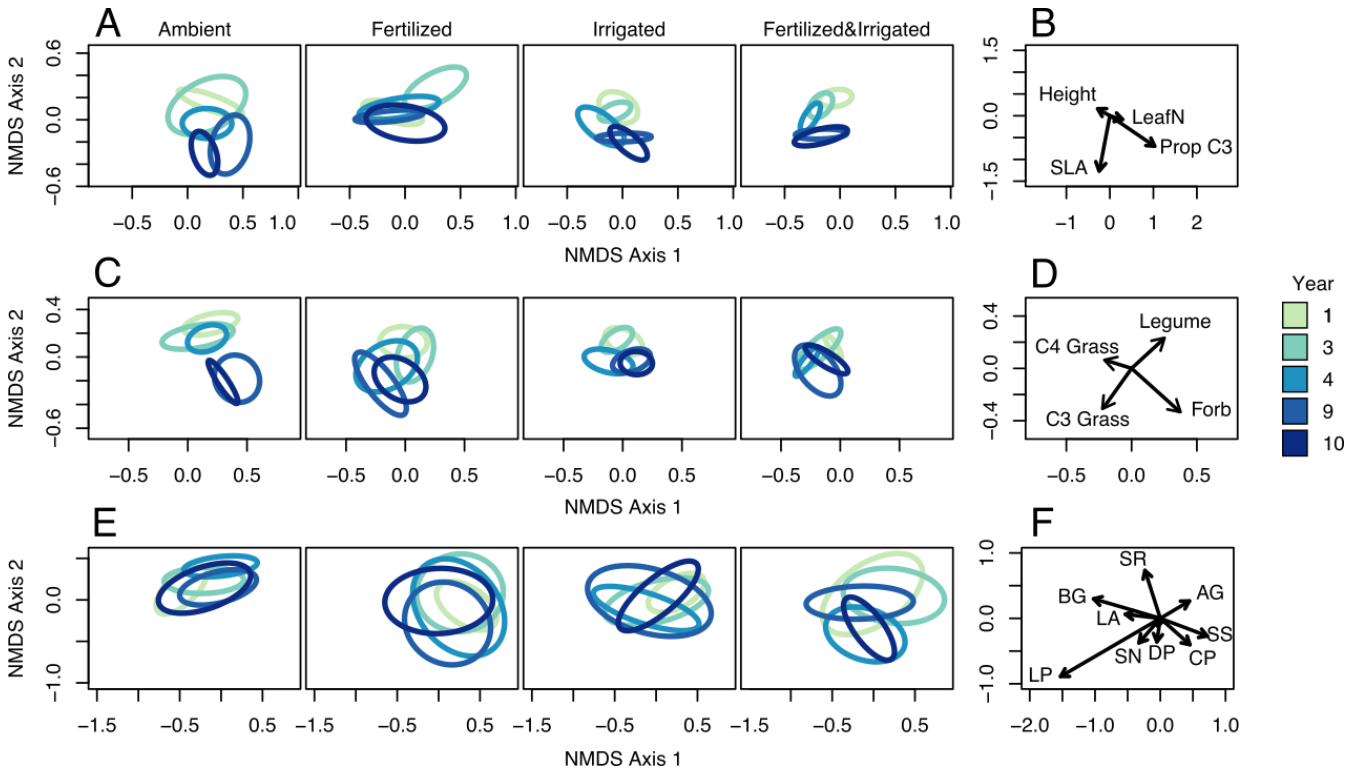


Figure 5: Abundance-weighted trait values show a clearer response to resource addition through time in multidimensional space. Upper panels show shifts in trait space (A,B), middle panels show shifts in functional group space (C,D), and lower panels show shifts in species community space (E,F). Loadings for traits (B), functional groups (D) and species (E, 10 most abundant shown) show the direction for increasing values. Axes are the top two non-metric multidimensional scaling (NMDS) axes, which represent most of the variation in trait, functional group, or taxonomic space. Traits used include specific leaf area (SLA), maximum vegetative height (Height), leaf nitrogen content per dry mass (Leaf N), and photosynthetic pathway (C3). Species abbreviations are AG: *Andropogon gerardii*, BG: *Bouteloua gracilis*, CP: *Coreopsis palmata*, DP: *Dalea purpurea*, LA: *Liatris aspera*, LP: *Lupinus perennius*, SN: *Sorghastrum nutans*, SR: *Solidago rigida*, SS: *Schizachryum scoparium*. *Poa parentis* is not shown in (F) because its arrow is in same direction as DP but much smaller in magnitude.

Appendix 1 - Supplemental Information

Table S1: Comparison of results using high N treatments (+14 g N/m^2/year) only, grouped N treatments (+7 or +14 g N/m^2/year), and both N treatments for species richness and functional dispersion as examples. The "*Fert*" row refers to either grouped treatments or the high N addition treatment depending on column heading. All other rows are as in Table 1 of main text. Values are effect size (standard error). *- p < 0.05, ** - p < 0.01, *** - p < 0.001

	Species Richness			Functional Dispersion		
	High N	Grouped N	Both N	High N	Grouped N	Both N
Intercept	22.42 (24.74) ***	20.62 (3.73) ***	20.62 (3.69) ***	0.13 (0.04) ***	0.13 (0.03)***	0.13 (0.03) ***
SPEI	6.78 (2.26) ***	5.69 (1.78) ***	5.69 (1.76) ***	-0.04 (0.02) ***	-0.04 (0.02)***	-0.04 (0.02) ***
Biomass	0.01 (0.005) ***	0.01 (0.004) ***	0.01 (0.004) ***	0.00001 (0.00004)	0.0000006 (0.00004)	0.000006 (0.00004)
Year	-5.07† (2.28)***	-3.99† (1.79)***	-3.99† (1.79) ***	0.03† (0.02)	0.03† (0.02)**	0.03† (0.02)**
Fert (+7 only)	---	---	-0.14 (1.39)	---	---	0.01 (0.01)
Fert	1.97 (1.43)	0.92(1.21)	1.97 (1.39)	-0.003 (0.001)	0.004 (0.01)	-0.003 (0.01)
Irr	0.94 (1.43)	0.85 (1.31)	0.85 (1.31)	0.003 (0.001)	0.007 (0.01)	0.007 (0.01)
Fert(+7 only):Irr	---	---	1.23 (1.61)	---	---	-0.03 (0.01) ***
Fert:Irr	0.40 (1.63)	0.82 (1.39)	0.40 (1.61)	-0.004 (0.01)	-0.02 (0.01) ***	-0.004 (0.01)
Fert(+7 only):Year	---	---	-1.74 (0.57) ***	---	---	-0.001 (0.01)
Fert:Year	-3.13 (0.61) ***	-2.43 (0.50) ***	-3.13 (0.57) ***	-0.003 (0.01)	-0.002 (0.01)	-0.003 (0.01)
Irr:Year	-1.34 (0.61) ***	-1.28 (0.47) ***	-1.28 (0.47) ***	0.003 (0.01)	0.0003 (0.004)	0.0003 (0.004)

772 *Table S2*: Datasets from TRY (request IDs: 4261 & 4354) and associated references. Note that
773 the five datasets with the most observations are from the Midwest region or from Cedar Creek
774 which accounts for over 50% of the trait data used from TRY.

Dataset	Reference	Observations
Midwestern and Southern US Herbaceous Species Trait Database	unpub.	1610
Plant traits of grassland species	(La Pierre and Smith 2015)	1538
Plant traits from Wisconsin, USA	unpub.	1050
Cedar Creek prairie plants (leaf, seed, dispersule, height, plant, root)	unpub.	671
Cedar Creek Savanna SLA, C, N Database	(Willis et al. 2010)	624
New York Old Field Plant Traits Database	(Siefert 2012)	584
The LEDA Traitbase	(Kleyer et al. 2008)	472
Plant Traits for Pinus and Juniperus Forests in Arizona	(Laughlin et al. 2010)	284
California Coastal Grassland Database	(Sandel et al. 2011)	216
The VISTA Plant Trait Database	(Garnier et al. 2007)	216
Plant Traits from LTER Matsch (Mazia), Italy	unpub.	200
FRED - Fine Root Ecology Database	(Iversen et al. 2017)	183
Eastern US Old Field Plant Traits Database	(Siefert et al. 2014)	170
Old fields of Eastern US (Siefert Data)	(Siefert et al. 2014)	170
GLOPNET - Global Plant Trait Network Database	(Wright et al. 2004)	162
Categorical Plant Traits Database	unpub.	155
Global Respiration Database	(Reich et al. 2008)	138
Rocky Mountain Biological Laboratory WSR/gradient plant traits	unpub.	119
Aboveground morphological traits of grassland species	(Abakumova et al. 2016)	110
Leaf and Whole Plant Traits Database	unpub.	97
French Alps Trait Data	(Gos et al. 2016)	89
Photosynthesis Traits Worldwide	(Maire et al. 2015)	79
Leaf Economic Traits Across Varying Environmental Conditions	(Wright and Sutton-Grier 2012)	78
French Massif Central Grassland Trait Database	(Louault et al. 2005)	72
Ecological Flora of the British Isles	(Fritter and Peat 1994)	71
Leaf and Whole Plant Traits Database	(Shipley 2002)	70
Flora Italia Functional Traits Hoard (FIFTH)	(Cerabolini et al. 2010)	69
Traits of 59 grassland species	(Schroeder-Georgi et al. 2016)	55
Grassland Plant Trait Database	(Takkis n.d.)	54
Reich-Oleksyn Global Leaf N, P Database	(Reich et al. 2009)	52
Italian Alps Plant Traits Database	(Bragazza 2009)	51
Leaf Physiology Database	(Kattge et al. 2009)	49
Global Respiration Database	(Atkin et al. 2015)	46
Leaf Allometry Dataset	(Price and Enquist 2007)	40
PLANTSdata USDA	(Green 2009)	33
Chinese Traits	(Prentice et al. 2011)	24
Plant Physiology Database	(Campbell et al. 2007)	24
Leaf Area, Dry Mass and SLA Dataset	unpub.	24
Northern mixed-grass prairie species traits - Wyoming, USA	unpub.	20
Traits of the Hungarian flora	(Lhotsky et al. 2016)	20
Plant Traits from Fynbos Forests in the Cape Region	(Onstein et al. 2014)	19
The DIRECT Plant Trait Database	(Fry et al. 2014)	19
BASECO: a floristic and ecological database of Mediterranean French flora	(Gachet et al. 2005)	18
The Netherlands Plant Height Database	unpub.	18
Leaf Structure, Venation and Economic Spectrum	(Blonder et al. 2012)	18
Photosynthesis and Leaf Characteristics Database	unpub.	18
Saskatchewan Plant Trait Database	(Guy et al. 2013)	18
Abisko & Sheffield Database	(Quested et al. 2003)	16
The Netherlands Plant Traits Database	(Ordoñez et al. 2010)	15
The Xylem/Phloem Database	(Schweingruber and Landolt 2005)	15
Sheffield Database	(Cornelissen et al. 1999)	14
Hokkaido leaf traits	(Mori et al. 2015)	13
PLANTATT - Attributes of British and Irish Plants	(Hill et al. 2004)	13
Sheffield-Iran-Spain Database	(Díaz et al. 2004)	13
The DIRECT Plant Trait Database	(Everwand et al. 2014)	11
Traits related to riparian plant invasion in South East Australia	(Catford et al. 2014)	11
Maxfield Meadow, Rocky Mountain Biological Laboratory - LMA	unpub.	10
Plant Physiology Database	(Loveys et al. 2003)	9

Plant Traits from Romania	(Ciocârlan 2000)	9
Abisko & Sheffield Database	(Cornelissen et al. 2004)	8
Leaf and Whole Plant Traits Database	(Meziane and Shipley 1999)	8
Nutrient Resorption Efficiency Database	(Vergutz et al. 2012)	8
Overton/Wright New Zealand Database	unpub.	8
TOPIC (Traits of Plants in Canada)	(Aubin et al. 2016)	7
Chinese Leaf Traits Database	(Han et al. 2004)	6
Functional Traits of Graminoids in Semi-Arid Steppes Database	(Adler et al. 2004)	6
Herbaceous Traits from the ÷land Island Database	(Hickler 1999)	6
Leaf N-Retention Database	(de Vries and Bardgett 2016)	6
The Americas N&P database	(Kerkhoff et al. 2006)	5
A Global Data Set of Leaf Photosynthetic Rates, Leaf N and P, and Specific Leaf Area	(Walker 2014)	4
Fonseca/Wright New South Wales Database	(Fonseca et al. 2000)	4
Leaf Traits and Seed Mass of Cover Crops	(Tribouillois et al. 2015)	4
Dispersal Traits Database	unpub.	3
Plant Coastal Dune Traits (France, Aquitaine)	unpub.	3
Functional traits explaining variation in plant life history strategies	(Adler et al. 2014)	2
Leaf and Whole Plant Traits Database	(Shipley and Lechowicz 2000)	2
Leaf Ash Content in China's Terrestrial Plants	(Han et al. 2012)	2
Leaf Traits Mount Hutt, New Zealand	(Kichenin et al. 2013)	2
Plant Physiology Database	(Atkin et al. 1997)	2
Plant Trait Database in East and South-East Asia	(Koike 2001)	2
Plant Traits of Acidic Grasslands in Central Spain	(Peco et al. 2005)	2
The Functional Ecology of Trees (FET) Database - Jena	(Wirth and Lichstein 2009)	2
Leaf and Whole Plant Traits Database	(Shipley 1995)	1
Leaf and Whole Plant Traits Database	(Shipley and Vu 2002)	1
Leaf and Whole Plant Traits Database	(Vile 2005)	1
Photosynthesis Traits Database	unpub.	1
Herbaceous Plants Traits From Southern Germany	unpub.	1
Mediterranean psammophytes	(Ciccarelli 2015)	1

Table S3: Percent trait coverage for height, leaf N content, and SLA. There was >89% coverage for all treatments each year. All species had a photosynthetic pathway, so coverage was 100% for all years and treatments.

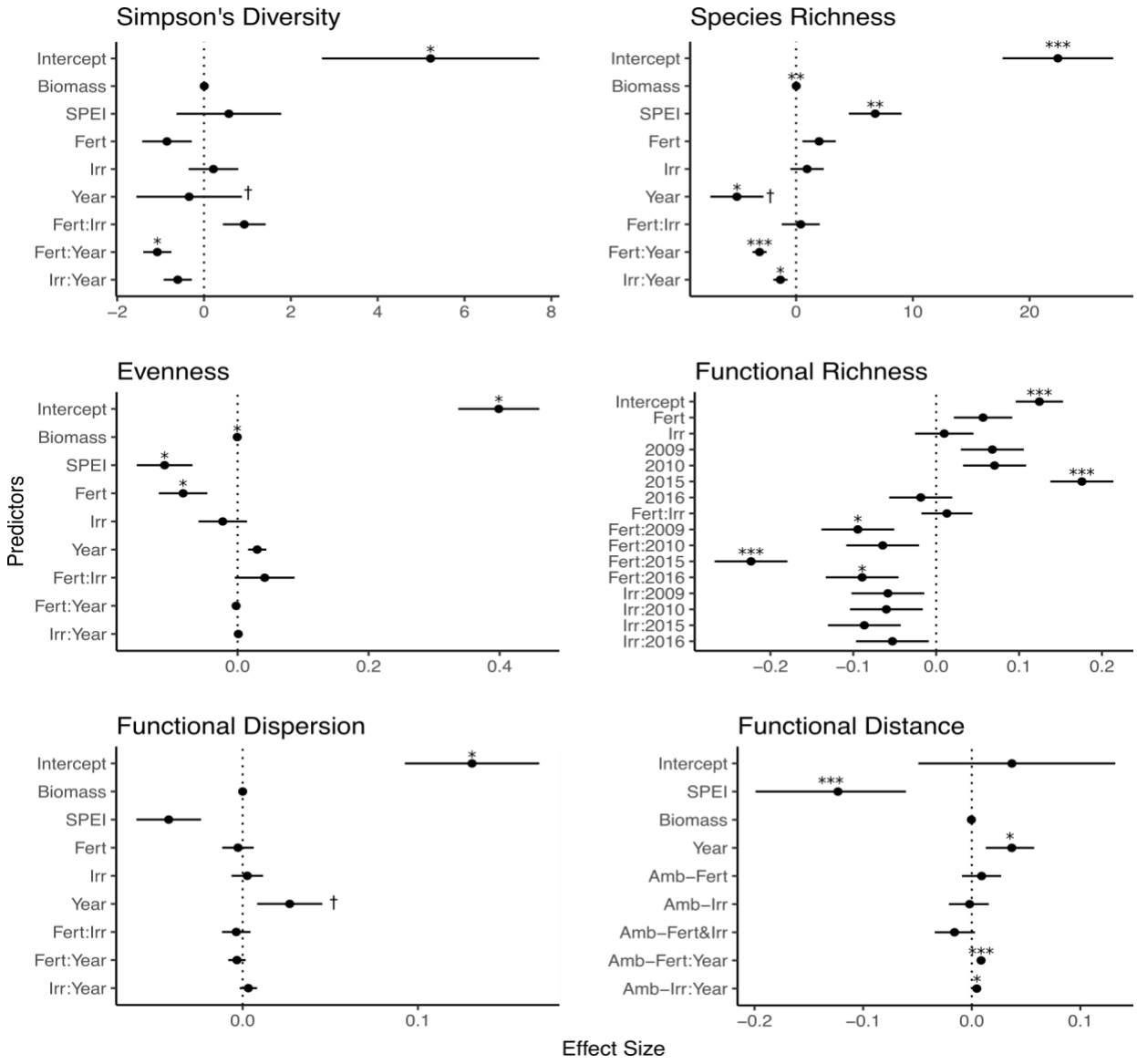
Year	N Treatment	Water Treatment	Species Coverage			Biomass Coverage		
			Height	Leaf N	SLA	Height	Leaf N	SLA
2007	ambient	ambient	100	100	100	100	100	100
	Fertilized	ambient	99.24	99.17	100	99.94	99.99	100
	ambient	Irrigated	99.24	99.24	99.24	99.99	99.99	99.99
	Fertilized	Irrigated	100	98.26	100	100	99.93	100
2009	ambient	ambient	98.55	97.57	99.28	99.64	99.97	99.99
	Fertilized	ambient	97.63	95.20	97.63	99.93	98.89	99.93
	ambient	Irrigated	100	100	100	100	100	100
	Fertilized	Irrigated	97.88	97.96	99.07	99.95	99.99	99.86
2010	ambient	ambient	96.64	87.30	96.64	99.933	99.63	99.99
	Fertilized	ambient	98.72	90.55	98.72	98.96	99.45	99.96
	ambient	Irrigated	100	97.36	100	100	99.51	100
	Fertilized	Irrigated	98.41	89.44	98.41	99.91	98.71	99.91
2015	ambient	ambient	97.86	89.44	97.86	99.97	89.11	99.97
	Fertilized	ambient	96.01	84.91	98.03	96.52	95.19	99.97
	ambient	Irrigated	97.54	89.06	97.54	99.95	92.73	99.99
	Fertilized	Irrigated	96.75	89.66	98.72	99.82	99.03	99.99
2016	ambient	ambient	96.96	94.52	96.96	99.85	99.25	99.85
	Fertilized	ambient	94.29	90.70	94.29	98.62	97.92	98.62
	ambient	Irrigated	99.12	98.43	99.12	99.99	99.96	99.99
	Fertilized	Irrigated	98.81	94.81	98.81	99.99	99.45	99.99

Table S4: Functional group biomass responds to both irrigation and fertilization treatments through time. Columns correspond with the individual functional groups. Models were run using the proportion of biomass characterized by the specified functional groups. Rows correspond to model parameters, --- means that those parameters were not included in the model. Values are effect size (standard error) *- p< 0.05, **- p < 0.01,*** - p < 0.001

	C4 Grass	C3 Grass	Legume	Non-legume Forb
Intercept	0.81 (0.11) ***	-0.09 (0.20)	0.74 (0.09)***	0.32 (.025)
SPEI	0.11 (0.07)	-0.16 (0.09) **	-0.122 (0.06)***	0.28 (0.18) ***
Biomass	0.004 (0.004)	-0.0003 (0.0002)	-0.001 (0.0004) ***	0.001 (0.0003) ***
Year	-0.06 (0.02) **	0.23† (0.10) ***	0.04 (0.02) **	-0.11† (0.12)
Fert	0.05 (0.06)	0.12 (0.06) ***	-0.16 (0.06) ***	0.14 (0.08) *
Irr	0.12 (0.06) **	0.16 (0.06) ***	-0.16 (0.04) **	0.09 (0.08)
Fert:Irr	-0.07 (0.07)	-0.11 (0.06) *	0.10 (0.07)	-0.15 (0.11)
Fert:Year	0.02 (0.01)***	0.03 (0.03)	-0.005 (0.006)	-0.18 (0.04) ***
Irr:Year	0.01 (0.01)	-0.06 (0.03) ***	0.02 (0.006) ***	-0.13 (0.04)***
Fert:Irr:Year	---	---	---	0.12 (0.06) **

Table S5: Fertilization either immediately impacts community weighted trait values or has a continuous effect whereas irrigation only has immediate and persistent effects. Output for the fixed effects of individual traits (columns), abundance weighted and not. Rows correspond to model parameters, --- means that those parameters were not included in the model. Values are effect size (standard error) *- p< 0.05, **- p < 0.01,*** - p < 0.001

	Abundance weighted				Non-Abundance weighted			
	SLA	Leaf N	Height	C3	SLA	Leaf N	Height	C3
Intercept	16.04 (0.44) ***	16.32 (1.06) ***	0.51 (0.09) ***	0.77 (0.11) ***	16.06 (0.33) ***	14.74 (1.49) ***	0.32 (0.05) ***	0.43 (0.10) ***
SPEI	----	-1.48 (0.74) **	0.10 (0.04) ***	-0.11 (0.07)	----	-1.92 (1.26)	0.13 (0.04) ***	-0.26 (0.07) ***
Biomass	----	-0.005 (0.004)	0.002 (0.0001) ***	-0.0004 (0.0004)	----	0.004 (0.004)	0.0006 (0.0001) ***	0.0002 (0.0004)
Year	-0.12 (0.04) ***	0.33 (0.24)	-0.05†(0.04)	0.06 (0.02) ***	-0.12 (0.04) ***	6.61 (13.45)	-1.14 (0.45)***	0.08 (0.02) ***
Year^2	---	---	---	---	---	-1.07 (4.36)	0.30 (0.11) ***	---
Fert	1.07 (0.60) *	-0.71 (0.60)	0.06 (0.03) *	-0.06 (0.06)	1.26 (0.44) ***	-0.50 (0.42)	-0.03 (0.02)	0.06 (0.06)
Irr	0.92 (0.51) *	-1.80 (0.60) ***	0.04 (0.03)	-0.12 (0.06) **	0.78 (0.44) *	-1.14 (0.42) ***	0.01 (0.02)	-0.04 (0.06)
Fert:Irr	-0.89 (0.65)	0.31 (0.71)	-0.10 (0.04) ***	0.07 (0.07)	-0.92 (0.55)	-0.04 (0.59)	0.02 (0.02)	-0.08 (0.09)
Fert:Year	0.07 (0.05)	-0.02 (0.07)	-0.05 (0.02) **	-0.02 (0.007) ***	0.05 (0.05)	-2.32 (2.70)	-0.13 (0.09)	-0.04 (0.01) ***
Irr:Year	-0.07 (0.05)	0.07 (0.07)	-0.02 (0.02)	-0.009 (0.007)	-0.05 (0.05)	0.26 (2.70)	-0.01 (0.09)	-0.02 (0.01) ***
Fert: Year^2	---	---	---	---	---	0.91(2.70)	0.04 (0.09)	---
Irr: Year^2	---	---	---	---	---	8.32 (2.70) ***	-0.22 (0.09) ***	---
Fert:Irr:Year	---	---	0.07 (0.02) ***	---	---	---	---	0.03 (0.01) ***



Supplemental figure 1: Fertilization continually impacts five of the six community metrics, whereas irrigation only significantly impacts two of six. Output from mixed effects models showing the impact of the fertilization and irrigation treatments on community metrics (panels) through time. The y-axis correspond to model parameters: SPEI is the standardized precipitation evapotranspiration index, Biomass is the average biomass across all plots for that year, Year corresponds to duration of experiment (0 = 2007, 9 = 2016), † in the year row indicates that the model was fit to the log of year, Fert is the nitrogen addition treatments and Irr is the irrigation

831 treatments. The x-axis is the effect size and error bars are standard errors, or in the case of

832 functional distance, 95% confidence intervals. *- p< 0.05, **- p < 0.01,*** - p < 0.001

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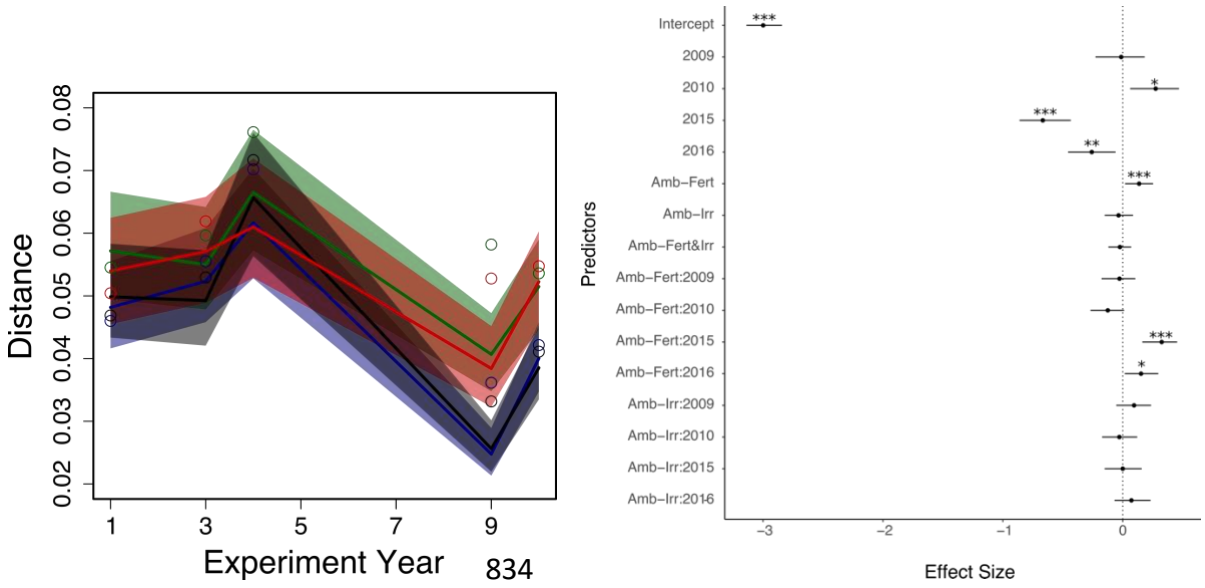

835 *Supplemental Figure 2:* Fertilization causes plots to becoming increasingly dissimilar when

836 considering non-weighted trait values, a stochastic effect (left). Points are means, lines are

837 estimated from the MCMCglmm output, and error bands are the upper and lower 95%

838 confidence intervals. The right panel shows the effect sizes and the 95% confidence interval for

839 each parameter in the MCMCglmm model. *- p< 0.05, **- p < 0.01,*** - p < 0.001

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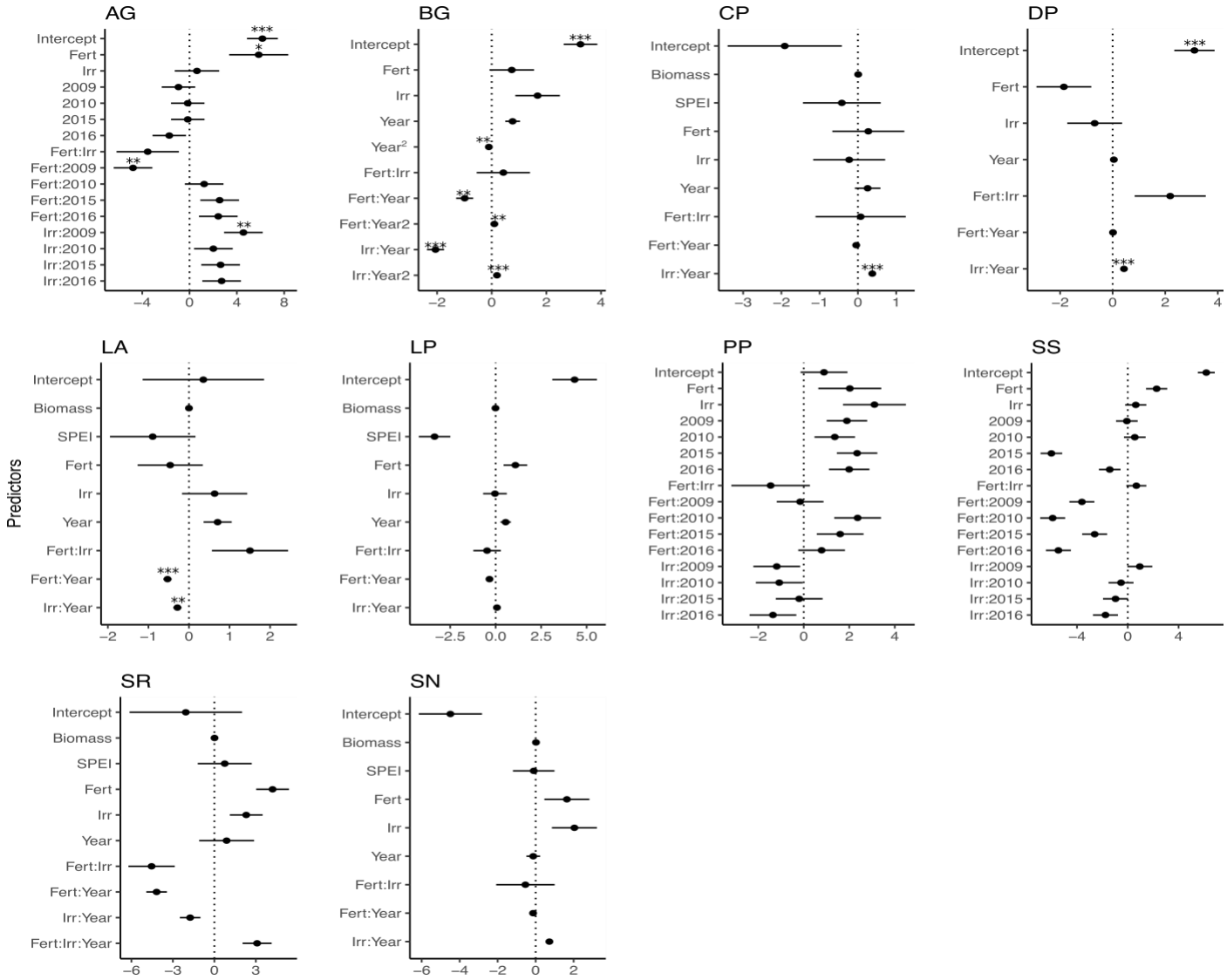

Figure S3. Most species responded in a gradual and continuous manner to either irrigation or fertilization. Output from mixed effects models showing the impact of the fertilization and irrigation treatments on community metrics (panels) through time. The y-axis correspond to model parameters: SPEI is the standardized precipitation evapotranspiration index, Biomass is the average biomass across all plots for that year, Year corresponds to duration of experiment (0 = 2007, 9 = 2016), † in the year row indicates that the model was fit to the log of year, Fert is the nitrogen addition treatments and Irr is the irrigation treatments. The x-axis is the effect size and error bars are standard errors, or in the case of functional distance, 95% confidence intervals. *- $p < 0.05$, **- $p < 0.01$,*** - $p < 0.001$. Species abbreviations are as follows - AG: *Andropogon gerardii*, BG: *Bouteloua gracilis*, CP: *Coreopsis palmata*, DP: *Dalea purpurea*, LA: *Liatris*

aspera, LP: *Lupinus perennius*, PP: *Poa parentis*, SN: *Sorghastrum nutans*, SR: *Solidago rigida*, SS: *Schizachryum scoparium*.

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